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Dental wear in dolphins (Cetacea: Delphinidae) from southern Brazil

Carolina Loch *, Paulo C. Simões-Lopes

Laboratório de Mamíferos Aquáticos, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, 88040-970, Florianópolis, Santa Catarina, Brazil

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ABSTRACT

(1) Dental wear is a common phenomenon in mammals. Its occurrence is influenced by tooth anatomy, animal physiology, biomechanics and behaviour. So far, investigations of dental wear in cetaceans have been scanty and superficial. We compare the frequencies of occurrence, location and intensity of dental wear in some species of dolphins from southern Brazil, South Atlantic Ocean. (2) Teeth of ten species were evaluated using a stereoscopic microscope to identify wear facets, which were classified according to location, anatomical position and wear intensity. (3) Frequencies of dental wear were high for all species with exception of *Delphinus capensis*, with less than 50% of teeth worn. Simultaneous wear facets in the apex and lateral of teeth were more common than facets restricted to the apex or lateral faces. Wear on the dental crown was more common, but some species showed less frequent wear down to the cingulum or root level. Superficial wear seems to be the general trend for dolphins, but *Stenella coeruleoalba* and *Pseudorca crassidens* showed a higher frequency of severe wear. Only for *Tursiops truncatus* the frequencies of wear were significantly different between males and females. When considering the ontogeny of dental wear, only for *T. truncatus* and *Stenella frontalis* indexes of dental wear were correlated with body length. (4) Whether dental wear has implications or not in fitness and feeding behaviour, severely worn teeth may expose the pulp cavity and increase the susceptibility to local infections.

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1. Introduction

Dental wear is consequence of a multifactorial process involving three synergistic components: attrition (effect of tooth-to-tooth contact), abrasion (friction against exogenous material, i.e. food items or tool use) and abfraction (micro-structural loss of dentine in stressed areas), and normally is related to age progression.¹

Variations in the morphology and structure of the tooth, biomechanics, animal physiology or behaviour may influence the nature and extent of tooth wear among different species of animals. Factors such as crown morphology, enamel

hypoplasia and lower resistance to wear, mastication mechanisms, consistency of diet and parafunctional uses of teeth are all potentially related to tooth wear.²

Tooth wear has been reported for captive or commercially valuable animals,^{3,4} early hominids and other primates^{5,6} and also fossil vertebrates.⁷ Numerous studies of tooth wear in wild mammals have been published in recent years, relating wear of dental tissues with life history aspects, feeding ecology, reproductive fitness, etc.^{8–11} However, the same is not true for those living in the aquatic environment. Dental wear has been reported in a few species of aquatic mammals, including sea lions, manatees and dolphins. Age progression,

* Corresponding author. Present address: Department of Geology, University of Otago, Dunedin 9054, New Zealand. Tel.: +64 03 479 8623.

E-mail address: carolinaloch@yahoo.com.br (C. Loch).

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Table 1 – Species, number of individuals, body length range and number of teeth analysed.

Species	Number of individuals	Body length range (cm)	Number of teeth analysed
<i>Delphinus capensis</i> (long-beaked common dolphin)	18	178–222	1690
<i>Lagenodelphis hosei</i> (Fraser's dolphin)	9	216–258	1032
<i>Orcinus orca</i> (killer whale)	3	378–397	68
<i>Pseudorca crassidens</i> (false killer whale)	4	370–523	104
<i>Sotalia guianensis</i> (Guiana dolphin)	205	83–203	17,867
<i>Stenella coeruleoalba</i> (striped dolphin)	8	212–243	869
<i>Stenella clymene</i> (Clymene dolphin)	2	198–200	188
<i>Stenella frontalis</i> (Atlantic spotted dolphin)	23	157–204	2033
<i>Steno bredanensis</i> (rough-toothed dolphin)	17	200–277	1055
<i>Tursiops truncatus</i> (bottlenose dolphin)	61	150–358	3071
Total	350	–	27,977

feeding strategies, behaviour and tooth mineral content were pointed out as factors influencing dental wear in pinnipeds.^{12–15}

In sirenians, both living and fossil, dental wear is closely related to their herbivore feeding habits.^{16–18}

Few previous studies mention the occurrence of dental wear in odontocete cetaceans,^{19–21} and in those studies inferences of causes and patterns were limited and simplistic. Detailed studies on the relationship of wear facets, diet and functional morphology were pursued for early ancestors of cetaceans,²² but there are few investigations focused in understanding trends and implications of tooth wear in modern dolphins. Caldwell and Brown²³ described patterns of dental wear in the killer whale (*Orcinus orca*) and related its occurrence with masticatory movements and feeding behaviour. On the other hand, Ramos et al.²⁴ related dental morphology and tooth wear to parameters such as sex, age and body length in the Franciscana (*Pontoporia blainvillei*) and Guiana dolphin (*Sotalia guianensis*). More recently, Foote et al.²⁵ observed distinct dental wear rates in different haplotypes of killer whales from the North Atlantic, suggesting that genetic and ecological divergence of populations may be reflected in dietary specializations and dental wear. The same idea was corroborated by Ford et al.,²⁶ relating the extreme wear of offshore killer whales with a diet based on sharks, prey that can be extremely abrasive on teeth.

This paper aims to evaluate the occurrence, location and intensity of macroscopic dental wear facets in dolphins (family Delphinidae) from the southern coast of Brazil, comparing and contrasting patterns of wear with sex and body length of the specimens. Potential causes and implications of dental wear to fitness of animals were also investigated.

2. Materials and methods

Teeth of 350 specimens representing 10 species of dolphins were analysed (Table 1). Specimens were accessed in five scientific collections from southern Brazil: Instituto de Pesquisas Cananéia (acronym IPeC); Museu de Ciências Naturais UFPR (MCN); Departamento de Ecologia e Zoologia UFSC (UFSC); Fundação Oceanográfica de Rio Grande (FURG) and Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul (GEMARS). Osteological material deposited in these collections came from stranded or accidentally entangled

animals, normally processed by water maceration or buried in sand.

Teeth were visually inspected under a stereoscopic microscope in order to highlight the wear facets. According to Thewissen et al.²² and Butler,²⁷ these facets are seen as smooth and flat surfaces evidenced by light reflection. Wear facets were categorized according to their location, anatomical extent and intensity, using dental anatomical terminology.²⁸

- Location: Apical, lateral or apical/lateral wear facets combined (Fig. 1a).
- Anatomical extent: Wear involving only the crown, or extending to cingulum or root (Fig. 1b).
- Intensity: Through wear indexes (Table 2, Fig. 2).

Worn teeth were evaluated and placed in each category (location, anatomical extent and intensity). Frequencies of prevalence were established taking into account the number of teeth affected and the total number of teeth analysed for

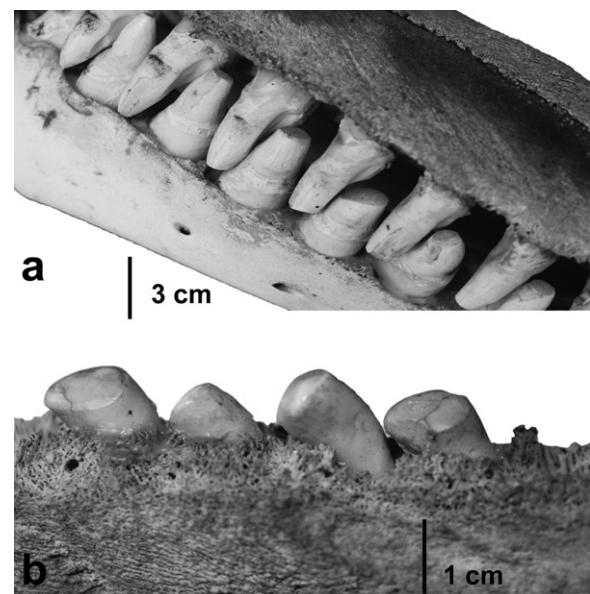


Fig. 1 – (a) Simultaneous apical and lateral wear facets in the false killer whale (*Pseudorca crassidens*, UFSC 1048) and (b) severe dental wear extending to the root level in the bottlenose dolphin (*Tursiops truncatus*, UFSC 1011).

Table 2 – Indexes of dental wear in cetaceans, based on diagnostic criteria and visual estimates of hard tissue loss.

Index	Wear intensity	Diagnosis
1	Superficial	Superficial wear, affecting enamel and exposing superficial dentine. Loss of a maximum of 10% of the crown area
2	Moderate	Moderate wear, exposing deeper dentine. Loss of crown area varies from 10 to 50%
3	Severe	Severe wear with more than 50% of loss of the crown area. Tooth cervix and root may be worn as well. Pulp cavity may be exposed in some cases

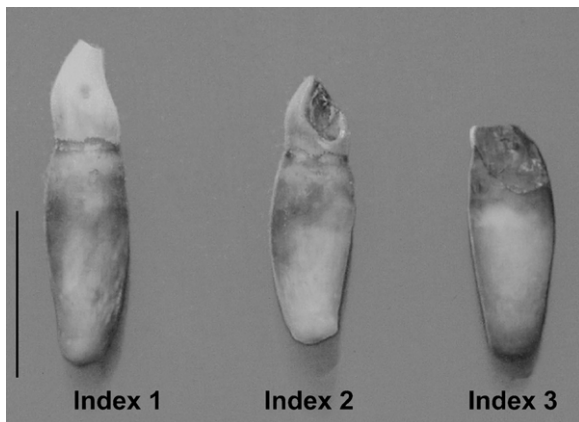


Fig. 2 – Categories of wear intensity in cetaceans (*Sotalia guianensis*, UFSC 1302). Scale bar = 1 cm.

each species. Data regarding sex and total length of specimens were obtained in the collections databases. Total body length (TBL) was used as a proxy for age of the specimens, as absolute age was not known. An independent sample Student's t-test was applied to evaluate the prevalence of dental wear between males and females. A correlation matrix followed by linear regression was used to test the association between prevalence of dental wear and body length of the specimens. Statistical significance was set at the 5% probability level.

3. Results

3.1. Prevalence of dental wear

Dental wear was observed in 92% ($n = 323$) of the individuals analysed in this study. All dolphin species evaluated were diagnosed with dental wear, but average prevalence frequencies varied among species (Fig. 3).

Wear frequencies were relatively high in all species and normally averaged around 70% or more. In dolphins with larger body size, such as killer whales (*O. orca*) and false killer whales (*P. crassidens*), wear frequencies were over 80% in both species. High wear frequencies were also observed in Clymene, spotted and striped dolphins (*Stenella clymene*, *Stenella coeruleoalba* and *Stenella frontalis*) which presented

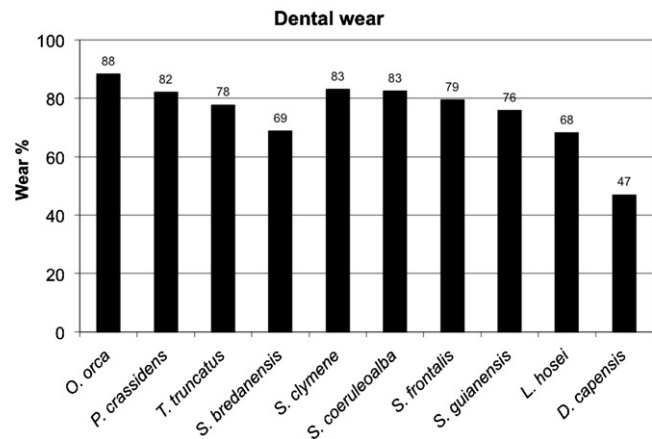


Fig. 3 – Dental wear prevalence in dolphins from southern Brazil.

frequencies between 79 and 83%. For all other species, wear frequencies were slightly lower. The long-beaked common dolphin *Delphinus capensis*, in particular, presented the lowest prevalence of wear among all species, with 47% of teeth worn.

3.2. Location of wear facets

Wear facets can be seen in the lateral faces of teeth (mesio/distal or buccal/lingual), on the apex, or occurring simultaneously in the lateral faces and apex (Fig. 1a). Simultaneous apical and lateral wear facets were more frequent among all species analysed, while isolated facets were comparatively less frequent (Fig. 4).

The general trend for dolphins seems to be wear occurring both in apical and lateral faces of teeth. All species presented frequencies higher than 20% in this category. When comparing wear in the apical or lateral facets isolated, no clear pattern is evident among species. The striped dolphin *S. coeruleoalba* showed the higher frequencies of apical wear, with 32% of teeth in this category. This was the only species where the frequency was over 20% for apical wear facets. On the other hand, killer

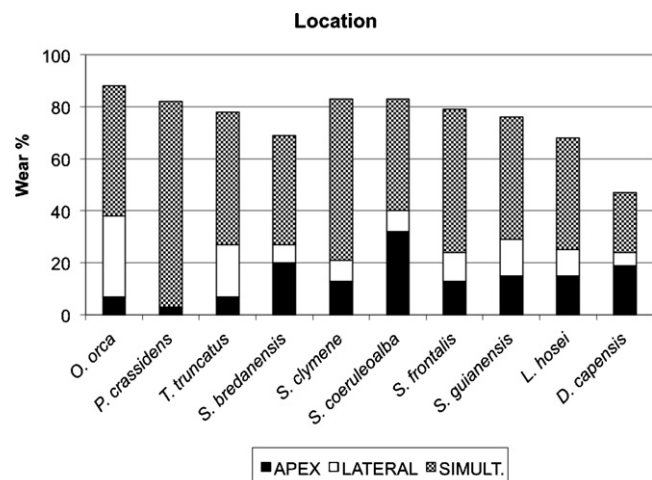


Fig. 4 – Location of wear facets (apex, lateral, simultaneous apex/lateral) in dolphins.

whales (*O. orca*) presented 31% of dental wear in lateral faces. However, sample sizes for both species are relatively restricted and conclusions should be drawn with prudence.

3.3. Anatomical extent

The dental crown was the anatomical region where dental wear was observed most frequently, with wear down to the cingulum or root level being less frequent or even insignificant (Fig. 5). Wear restricted to the crown was common (80% or less) in Fraser's dolphin *Lagenodelphis hosei*, Guiana dolphin *S. guianensis* and striped dolphin *S. coeruleoalba*. The latter two species had coronal wear in more than 70% of the sample. Conversely, in killer whales (*O. orca*) and false killer whales (*P. crassidens*) a relatively high percentage of teeth were worn down to the cingulum level. Teeth worn down to the root level were registered in relatively high frequencies (over 40%) in two species with distinct body and tooth size, the false killer whale *P. crassidens* and the much smaller Clymene dolphin, *S. clymene*.

3.4. Intensity of wear

Superficial wear (Index 1) was commonly observed in dolphins and, for most of the species, was registered in more than 40% of the teeth (Fig. 6). Only for the false killer whale the superficial wear was less frequent than moderate (Index 2) and severe wear (Index 3). Superficial wear (Index 1) was relatively important for the Guiana dolphin *S. guianensis*, striped dolphin *S. coeruleoalba*, Fraser's dolphin *L. hosei* and killer whale *O. orca*. In these species 60% or more of the teeth were worn superficially.

Moderate (Index 2) and severe wear (Index 3) were registered less frequently for most dolphin species. Only for the Clymene dolphin *S. clymene*, false killer whale *P. crassidens* and Atlantic spotted dolphins *S. frontalis*, moderate and severe wear were relatively conspicuous and registered in more than 20% of the teeth.

3.5. Sexual dimorphism in dental wear

Differences in dental wear prevalence among males and females were assessed only for the Guiana dolphin

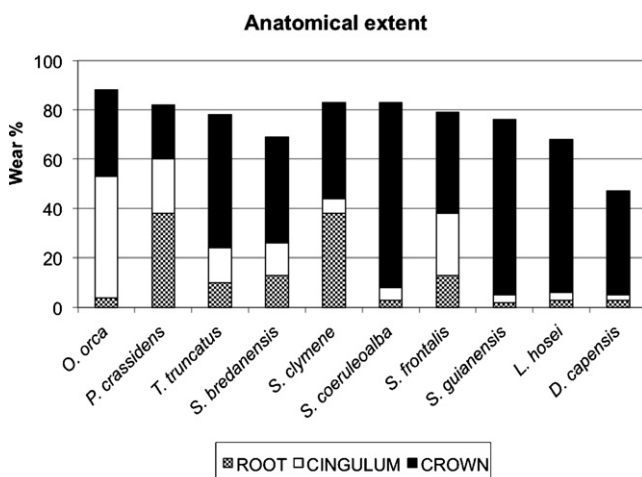


Fig. 5 – Anatomical extent of dental wear facets in dolphins.

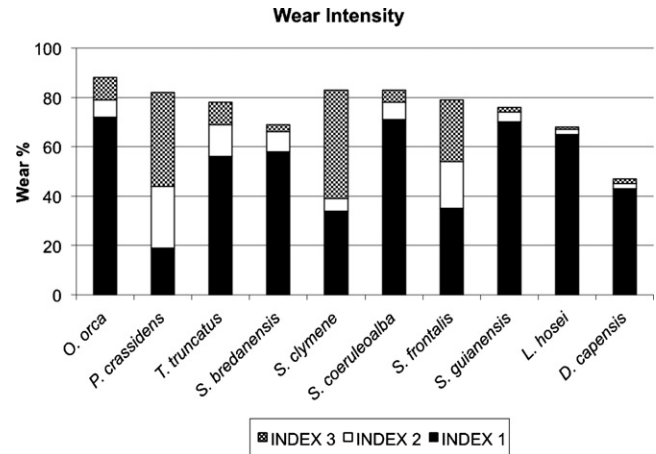


Fig. 6 – Frequencies of dental wear intensity in dolphins.

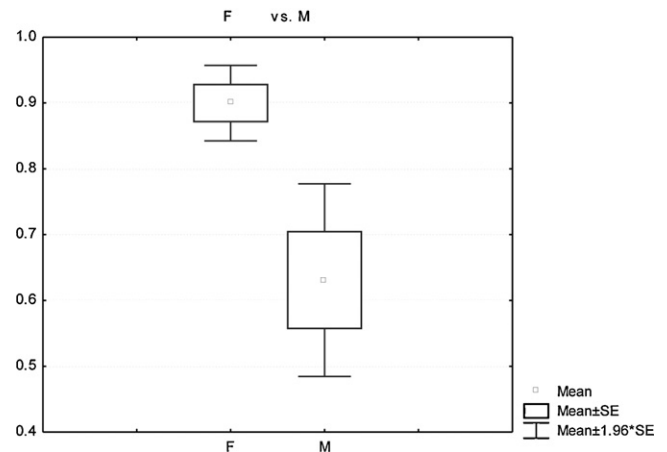


Fig. 7 – Variation in dental wear prevalence among females and males of the bottlenose dolphin *T. truncatus*.

S. guianensis and bottlenose dolphin *Tursiops truncatus*. Other species had few individuals of known sex.

In the Guiana dolphin, frequencies of wear were statistically similar among males and females ($t = 0.3597$; $p = 0.7196$). Males presented an average wear prevalence of 77% of their teeth ($SD = \pm 31$), and females of 75% ($SD = \pm 33$). On the other hand, wear frequencies were statistically different in males and females of the bottlenose dolphin ($t = 3.1659$; $p = 0.0029$). For this species, females had an average of 90% of their teeth worn ($SD = \pm 13$), while for males the average was 63% ($SD = \pm 35$) (Fig. 7).

3.6. Dental wear and ontogeny

The association between indexes of wear intensity (Indexes 1–3) with the total body length (TBL) of the specimens was tested using a correlation matrix. This analysis was performed only for the long-beaked common dolphin *D. capensis*, Fraser's dolphin *L. hosei*, Guiana dolphin *S. guianensis*, Atlantic spotted dolphin *S. frontalis* and the bottlenose dolphin *T. truncatus*, species that had a sufficient number of individuals with

Table 3 – Linear regression between total body length (TBL) and indexes of dental wear intensity (Indexes 1–3).

Species	TBL X I1		TBL X I2		TBL X I3	
	R ²	p	R ²	p	R ²	p
<i>D. capensis</i> (n = 9)	–	–	–	–	–	–
<i>L. hosei</i> (n = 9)	–	–	0.61	0.007 ^a	–	–
<i>S. guianensis</i> (n = 121)	0.23	0.000 ^a	–	–	–	–
<i>S. frontalis</i> (n = 13)	0.42	0.009 ^a	0.37	0.015 ^a	–	–
<i>T. truncatus</i> (n = 32)	0.40	0.000 ^a	0.43	0.000 ^a	0.21	0.004 ^a

^a Statistically significant.

known TBL. In cases where the variables showed statistically significant correlation, a linear regression was applied (Table 3).

The linear regression evidenced that only for the bottlenose dolphin *T. truncatus* all three categories of wear intensity showed a positive relationship of dependence with the TBL. This result in an increase of wear indexes with increasing of body size. For the Atlantic spotted dolphin *S. frontalis*, only indexes of superficial (Index 1) and moderate wear (Index 2) increased with body size. For the other species evaluated, results were distinct. The Guiana dolphin *S. guianensis* presented a positive dependence of wear intensity and body size only for superficial wear (Index 1), while in Fraser's dolphin *L. hosei* this relationship was observed only for moderate wear (Index 2). No relationship of dependence among wear intensity and body size was established for the long-beaked common dolphin *D. capensis*.

4. Discussion

Dental wear is a common phenomenon in mammals.^{3,4,7–11,29–31} In cetaceans, the high prevalence of wear among the group contrasts with the scarcity of published studies, where the scope normally was focused on a topic other than teeth, and dental wear was incidentally documented.^{19,21,24} However, cetaceans with worn teeth were important for the first taxonomic studies of odontocetes. The original description by Montagu of the bottlenose dolphin (*T. truncatus*) was misled by the severely worn teeth of the type specimen ('truncated teeth').¹⁹ A similar situation was observed with the description of the type-specimen of *Delphinus tursio obtusus* Schlegel, 1870, now a synonym of *T. truncatus*. The original description was based in an old specimen with teeth heavily worn.³²

The occurrence of dental wear is influenced by the use of teeth throughout life.^{9,11,23,30,33} Food consistency and hardness of enamel, which can vary among individuals, are also very important in the genesis and progression of dental wear.³⁴ In most heterodont mammals, teeth from the lower and upper jaw fit precisely and closely together through the occlusion of cusps and fossae of cheek teeth.² On the other hand, in dolphins and other cetaceans, the upper and lower teeth interdigitate, but generally do not occlude to masticate food, which means teeth are important in food acquisition but have limited function in food processing.³⁵ The tooth-to-tooth contact generated when upper and lower teeth fit in between each other when the jaw is closed is potentially the main source of dental wear for cetaceans.²⁰ Aggressive behaviours

such as jaw clapping and biting which results in tooth rate marks could also contribute to dental wear in dolphins, due to increased abrasion and teeth more prone to breakage and posterior wearing.³⁶

Worn teeth were registered in all species evaluated, with some high frequencies of prevalence. *D. capensis* was the only species where the frequency was lower than 50%. The highest frequencies were registered in Globicephalinae (*O. orca* and *P. crassidens*), species with less teeth in the upper and lower jaws but with teeth absolutely much bigger in size.^{2,23,37} The opposite trend was observed in *D. capensis*, a species with long rostrum, many teeth per quadrant and teeth relatively smaller and thinner than other Delphininae. Due to the smaller size and diameter of teeth in *D. capensis*, mesio-distal surfaces of upper and lower teeth are not always sliding over each other when the jaw is closed. On the other hand, the bigger and heavily built teeth of *O. orca* and *P. crassidens* are always in contact when jaw is closed and teeth interdigitate. This observation suggests that the interdigitation contact play a major role in the occurrence of attritional dental wear.

Mastication is the most common method of food processing in mammals, where a combination of three main movements (vertical, lateral and circular) promotes the contact of occlusal surfaces of lower and upper teeth.^{23,38,39} In dolphins, food processing results from limited mastication²³ combined with a component of suction feeding.⁴⁰ However, mastication and occlusal contact are probably far less prominent in cetaceans than in many terrestrial mammals. During food processing, dolphins use mainly the vertical movements of jaws, but lateral and circular movements may also be executed less prominently.²³ The repeated tooth-to-tooth contact between the margins of teeth when the lower jaw is closed is considered the main cause of lateral wear facets, mainly in the mesio-distal surfaces.^{22,41} Direct opposition of teeth during less prominent lateral and circular movements could be responsible for apical wear. In this case, food apprehension could also have a role in wearing down the apex of teeth by abrasion.^{23,26}

Simultaneous wear in the tooth apex and lateral margins were frequent in dolphins in our study, reinforcing the role of limited jaw movements and dental interdigitation as main generators of dental wear. Wear facets restricted to the apex or lateral faces isolated were less frequent in our sample. As reported in previous studies, simultaneous apical/lateral wear facets were also common in museum specimens of several other mammal groups.⁴¹

Wear under the gum line is not uncommon in delphinids,^{20,21,23} indicating that tooth tissues below the crown may

be affected. The tooth cingulum and root, which are covered by the periodontium and are encased in the alveoli, proportionally were less worn than the dental crown. Coronal wear facets were the most frequent in our study, with exception of the Globicephalinae species *O. orca* and *P. crassidens*, where wear facets down to the cingulum and root level were relatively common. Even if we consider the small sample sizes of these species, it is important to mention that tooth morphology and feeding behaviour should be influencing not only the high wear rates, but also the extension of worn areas. The relatively larger cingulum and roots of *O. orca* and *P. crassidens* would be more susceptible to dental wear than those species with smaller teeth, as the mesio-distal surfaces worn by tooth-to-tooth attrition could more easily be extended towards the cingulum and root.² Ford et al.²⁶ related the extreme dental wear observed in offshore killer whales to a diet based on sharks, in contrast with the minor or negligible wear of resident and transient killer whales, whose diet is based on fish and marine mammals, respectively. Unfortunately we cannot compare the diet and wear patterns of our sample of killer whales, due to lack of information on feeding habits of the sampled individuals.

The use of visual indices to estimate the intensity of dental wear has been proposed for several other mammal species, including humans,⁴² bears,^{9,29} lemurs^{10,30} and sea lions.¹⁴ Although differences in tooth shape among mammalian taxa have lead to the establishment of distinct categories of dental wear, principles adopted are similar and rely on standardization of criteria by the researcher. In odontocete cetaceans, homodonty and absence of cusps or other morphological features facilitates and simplifies the standardization of categories by using the estimated percentage of tooth loss.²⁶

In our study, superficial wear was frequent in all species of dolphins with exception of the Clymene dolphin *S. clymene* and false killer whale *P. crassidens*. However, besides having small sample sizes, sampled specimens of both species were most likely adults due to their body length (see Table 1), a factor that could explain higher frequencies of moderate and severe wear in these species. For most of the other species analysed, although general prevalence of wear was high, wear was mostly superficial and affected enamel and outer dentine. This observation is consistent with the limited role of dolphin teeth in food processing and modified occlusion resulting in interdilatation contact.³⁵ It is expected that the natural progression of wear will generate moderately to severely worn teeth. While superficial wear would have limited or negligible implications for the fitness of individuals, moderate and severe wear could have the potential to expose the pulp cavity and lead to tissue necrosis and increase the susceptibility to infections.^{30,41}

In general, the occurrence of dental wear is related to progression of age.^{9,11,19,20,23} In *S. guianensis*, Ramos et al.²⁴ observed that the height of the tooth crown and the height of the tooth itself were negatively related to the age of specimens, due to the higher prevalence of wear. Using the total body length (TBL) of individuals as a proxy to estimate age, we observed that our sample of *S. guianensis* did not follow the same trend established by Ramos et al. For our specimens, superficial wear was frequent even in bigger and potentially older animals. The weak association between indexes of wear

and body size of specimens of *D. capensis*, *L. hosei* and *S. guianensis* suggests that, at least in these species, dental wear is common among all body sizes and age ranges and it is not influenced by growth and ageing processes. It would be expected that in those cases, interdilatation contact of upper and lower teeth played a more important role in generating dental wear than abrasion due to tooth use. Besides, allometric growth of teeth and body should also be taken into consideration. It means that different body parts may grow at varying rates during lifetime and could explain the weak association between dental wear and body size in these species.

S. frontalis and *T. truncatus* showed a similar trend regarding the intensity of dental wear and body length of individuals. Frequencies of superficial, moderate and severe wear increased with body size. The same trend was observed for North Atlantic killer whales.²⁵ Only these latter two species corroborated the pattern of increase in frequency of dental wear with ageing and growth.^{9,11,19,20,23} Statistical analysis showed that these variables were dependant, but determination coefficients were not high. This may suggest that other factors besides growth and ageing may be influencing dental wear in cetaceans, as observed with populational differences in dental wear for killer whales in the Northern hemisphere.^{25,26}

Theoretically, one would expect equal prevalence of tooth wear for both sexes.^{23,30,43} Ramos et al.²⁴ did not find differences in tooth measurements between sexes in *S. guianensis*, suggesting a homogeneous prevalence of dental wear. The same was observed with *S. guianensis* in our sample. On the other hand, in our study females of the bottlenose dolphin (*T. truncatus*) presented higher wear frequencies than males. Although there may be behavioural particularities that could explain the differences observed, it is also possible that this difference is related to changes in physiology. In some bat species, resorption of calcium is high in females during lactation and prolonged hibernation, which could provoke changes in hardness of dental tissues and lead to fractures and more susceptibility to wear.⁴⁴ The same phenomenon is well known for pregnant women, whose skeleton is remodelled with loss of bony tissue due to transferring of serum calcium to the foetus during gestation and later during lactation.^{45,46} For a few species of dolphins, resorption of dental tissues leading to internal and external changes has been related to regulation of blood serum calcium due to stressful events such as parturition.⁴⁷ However, it remains unclear why only females of *T. truncatus* have higher wear rates, if the same physiological dynamics is expected to happen in females of other dolphin species. This issue is still poorly understood and deserves further investigation.

Dental wear in dolphins needs further study and understanding, as observed with the difficulties in explanations noted above. Variation among species in relation to frequencies of prevalence, intensity and anatomical extent also need to be better understood. However, our results include one of the first detailed accounts of dental wear in several species of dolphins, animals with specialised tooth morphology and distinct functional and biomechanical demands in comparison to terrestrial mammals. As observed with most wild mammals, dental wear is a normal physiological process derived from teeth usage throughout life and most likely it

does not reflect health and physical condition.^{8,10,30} Thus, it is expected that healthy cetaceans would show some degree of dental wear during their lives, as a consequence of the interdigitation contact of teeth and their feeding behaviour.²³ In some cases, specimens with severely worn teeth show signs of good physical condition, suggesting limited health and functional implications.^{8,10,23,26,30} Nonetheless, severe and progressive wear may expose the pulp cavity and increase the susceptibility to infections such as osteomyelitis, potentially compromising the performance and fitness of animals.^{20,41,48,49}

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Competing interest

None.

Ethical approval

This study used osteological material deposited in museums, so no research was performed on live animals. Ethical approval was not required.

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